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GENETICS



of LOBLOLLY PINE



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SUMMARY

Loblolly pine is the most important species in the southern pine region because it makes up about half the softwood volume. It is intensively managed on many, large, forest landholdings. The wood is used for timber, poles, lumber, pulp, and veneer.

The species has been widely studied, and 148 references covering sexual reproduction, vegetative reproduction, geographic variation, tree-to-tree variation, interspecific hybridization, and seed orchards have been reviewed.

Loblolly pine may start seed production at 3 to 4 years and reach sexual maturity at about 10 years. Flowers of both sexes are produced on the same tree, pollen is transported by the wind, selfing is minor, seed production is high, controlled pollination is relatively easy, and seed may be stored for many years—all of which facilitates intensive breeding.

Propagation of clones for seed orchards is by grafting, but small numbers of trees have been produced by rooting cuttings or air layers. Rooting needle bundles is extremely difficult.

Geographic variation is clinal for some economically important traits. Trees from coastal areas generally grow faster than those from inland areas. Recommendations for the better sources of seed for planting in various geographic areas are kept current as results are obtained from range-wide studies and intensive studies of a State or two-State area.

Tree-to-tree variation is wide for many economically important traits and is continuous or forms a gradient. Undesirable traits may form gradients, also. However, phenotypes free of defects such as disease attack, stem forking, excessive stem crook, and unfruitfulness occur. Selection can be directed toward

defect-free trees instead of trees with a lower-than-average degree of defect.

Resistance to pests varies among geographic locations and among trees within stands. Resistance to rust does not always increase with rate of growth in individual trees. Wood characteristics vary to a small degree among geographic locations and to a larger degree among trees. Crown and stem form vary from poor to good among individual trees.

Relationships among economically important traits are such that selection for each trait is required. Certain traits such as resistance to rust and volume growth are cumulative and increase yield per acre, and it seems possible to improve growth rate without loss of tree or wood quality.

Natural hybrids of loblolly pine with longleaf, shortleaf, pond, slash, and pitch pines have been noted within and among geographic locations. Hybrids of loblolly pine with pitch pine are commercially important in Korea. In the United States, hybridization is experimental but may be useful in increasing resistance to disease. In hybrids, many traits are intermediate with those of the parental species, and seed yield may be low.

Breeding programs with loblolly pine are widespread throughout the range of the species and promise significant increases in wood yield. A large proportion of planting stock is from seed of clonal seed orchards. Establishment of second-generation seed orchards with the most outstanding trees and clones available is underway. Selection is based on an index that may include 10 to 12 of the most important traits. Selection of seed orchard clones may be among trees of the best families, local stands, or geographic races.

Genetics of Loblolly Pine

Keith W. Dorman¹ and B.J. Zobel²

INTRODUCTION

Loblolly pine (*Pinus taeda* L.) is the most important species, on the basis of geographic distribution and timber volume, of the group known as the southern yellow pines in the southeastern United States. It has received monographic treatment (Mohr 1897; Wahlenberg 1960) related to its ecology, silviculture, and utilization. The species is important to tree breeders because it is used for extensive planting in southern Africa, South America, and Australia (Burley 1967).

Loblolly pine is in the Subsection *Australes*, which contains eight species in the southeastern and eastern United States, two in the West Indies, and one in both the West Indies and adjacent Central America (Critchfield and Little 1966). Abundance of closely related species has enhanced opportunities for interspecific hybridization.

Loblolly pine is diploid and generally stable in regard to polyploidy. Chromosomes of the major southern pine species are similar (Saylor 1961). Mutant alleles carried in the heterozygous condition were revealed as a result of controlled selfing (Franklin 1969b); abnormal color of cotyledons and of primary and secondary needles and also morphological abnormalities in seedlings were found to be common. Chromosomal structure was found to be slightly more irregular in interspecific hybrids than in parent trees (Saylor 1967).

Loblolly pine is a strongly multinodal species that begins rapid height growth at 3 to 5 years of age and

grows rapidly through years 20 to 30. Site conditions strongly influence volume production, but the species occurs both on moist soils in coastal areas and on much drier sites in the Piedmont and West Gulf Coast. Its range extends from sea level to an elevation of about 1,200 feet in Tennessee. Loblolly pine is widely planted, and it occurs in natural, pure stands and in mixed stands with other pines and hardwoods. Rotation ages range from 15 to 45+ years, depending on site and end product desired.

The heavy, strong wood is used for a wide variety of products, and its quality characteristics have received much attention from wood scientists. Wood qualities have been included in breeding programs along with pest resistance, improved growth and form, and adaptability. Loblolly pine is ideal for genetic manipulation; it has great variability because of its wide geographic range and the many environments in which it grows. It also has much variability within stands. Because heritability of many of the differences has been found to be reasonably high, progress can be made from a breeding program. It appears to be a "promiscuous" species that hybridizes with several others but still retains its identity as loblolly pine.

Because of the importance of this species and because it has several undesirable characteristics, such as poor form, a great deal of effort has been expended to improve it genetically. Loblolly pine is one of the better known coniferous trees, genetically speaking. Considerable improvement in growth, form, wood, and adaptability has been made, and second-generation breeding is already underway. In addition to the large acreages of commercial orchards, specialty orchards for problems such as disease resistance, drought, specialty woods, etc., have been established.

¹ Principal Silviculturist, USDA Forest Service, Southeastern Forest Experiment Station, Asheville, N.C.

² Professor of Forest Genetics, North Carolina State University, Raleigh, N.C.

SEXUAL REPRODUCTION

Reproductive Development

Loblolly pine is monecious, but sometimes bisporangiate strobili are produced that are male at base (Zobel 1952). Individual seedlings may produce

isolated conelets at 3 or 4 years of age (Greene and Porterfield 1962), but consistent flowering¹ occurs

¹ It is recognized that the "flower" is a strobilus, but this structure is commonly referred to as a "flower" by foresters and will be so referred to in this paper.

after age 10 to 15 in open stands and somewhat later in closed stands. Flowering in grafted seed orchards occurs earlier than in seedlings, with numbers sufficient for controlled pollination at 2 or 3 years and commercially important volumes of seed at 7 years (Bergman 1968).

Primordial flower buds are formed during early summer after the middle of June, and staminate flower buds can be seen in October and November as small knobs around the base of vegetative buds. Female flower buds are first indicated by swelling on the apex of vegetative buds in late fall or winter. They develop rapidly in warm spring temperatures and require close observation if controlled pollination is to be performed at the proper time. Development of flowering parts follows the seasonal pattern described for slash pine (Mergen and Koerting 1957).

Loblolly pine conelets are borne singly or in groups of two to six on twigs in the upper crown. They do not always develop uniformly throughout the tree. Conelets may reach full development a few days before or after pollen release, depending on weather conditions. Time of pollination within one tree usually lasts only a day or two but takes place over several weeks within a stand. Flowers of individual trees develop at greatly different rates, making for nonrandom pollination within a stand or seed orchard.

Seed yield per cone is usually good. Cones from one seed production area contained an average of about 90 seed, and a few trees had as many as 135 seed per cone (VanHaverbeke and Barber 1964). Usually, a yield of 30 to 40 seed per cone is considered normal, but individual trees will vary from 3 or 4 to as many as 180 seeds per cone.

In seed orchards, flowering and cone ripening vary widely, with the period of maximum receptivity of conelets occurring for some clones before it starts in others (Wasser 1967; Bergman 1968). Cone ripening may vary over a 50-day period, with cones opening over a 46-day period (Zoerb 1969). In early-ripening clones there may be 20 days between cone maturity and opening, but in late-opening clones this period may be only 10 days. Speed of opening is largely dependent on weather conditions and is most rapid when warm days and cool nights occur during a period of low relative humidity. Observations indicate that differences in cone production and seed ripening, apparent in natural stands and seed production areas, have a genetic basis (Thorbjornsen 1960) and should be considered for inclusion in tree selection criteria. These differences are important because, as Bergman (1968) points out, one clone could produce as much as 50 percent of the seed in a 10-year-old seed orchard. Selection for fast growth and early flowering followed by controlled pollination in seedlings up to 4 years old produced progeny of good vigor that flowered at 2 years of age (Greene 1969).

In the southern part of its natural range in Florida, flowers are receptive in mid-February, but in the more

northern latitudes of Virginia they may not be ready for pollination until mid-April (Dorman and Barber 1956).

Seed production is generally good but varies from year to year. Because of losses to pests or freezes, cone crops often are more variable than is flower production. Pollination is by wind, and heavy rain and sub-freezing temperatures often reduce conelet retention. A large part of the seed crop is sometimes destroyed by squirrels. Seed size varies widely because of both environmental and genetic factors. The effect of seed size on seedling growth is not sufficient to be a factor in long-range progeny testing, but it can have a marked effect on short-term experiments and must be considered for greenhouse or field tests that last for only a year or two.

Collection of seed after cone maturity is desirable because seed germinates best when so collected and cones often caseharden if picked too early. Loblolly pine seed generally requires stratification, although dormancy is variable among individual trees, and some lots actually germinate less well following stratification. The standard test with 20-weight oil for cone maturity works well, and cones with specific gravities of 0.88 or less will open upon drying (McLemore 1959).

Cross- and Self-Pollination

Normally, loblolly pine is a cross-pollinating species. The pollen is airborne, with the ovulate cones normally being found in the upper crowns and the staminate in the lower crowns. However, open-grown trees with large crowns often do not have a clear separation of sexes, and ovulate cones can be produced near the ground. In the middle crown, both staminate and ovulate cones commonly occur together.

The effect of selfing in clonal seed orchards has been of concern because it lowers seed yield, seed germination, and seedling growth (Franklin 1969a). However, in the presence of adequate volumes of pollen—such as would occur in seed orchards after they pass the establishment phase and male flower production becomes abundant—selfing may be less serious, although this has not been thoroughly studied. In a natural stand of loblolly pine, frequency of self-fertilization was 2 percent in the upper crowns and 31 percent in the lower crowns (Franklin 1969a).

Controlled self-pollination in loblolly pine has indicated that a number of mutant alleles are carried in natural populations, some of which may be useful as genetic markers (Franklin 1969b).

Controlled Pollination

Pollination in loblolly pine is successful when carried out according to methods described for other pines (Cumming and Righter 1948; Mergen, Rossoll,

and Pomeroy 1955; Goddard and Allen 1955). Modification is sometimes used for isolation bags, pollen extractors, pollen applicators, and marking labels, but the general methods are similar. On vigorous grafts, loblolly pine shoots elongate rapidly and require large bags to cover them without damaging conelets.

Pollen can be collected shortly before normal shedding. Such collections may be made when the first catkins on a tree are opening or when a yellow fluid can be produced by squeezing the staminate catkin or after the yellow phase when a clear liquid is exuded. Pollen catkins should be dried quickly; plastic sausage casings have proved to be suitable as containers for pollen extraction. Impurities in the shed pollen can be removed by straining through a 60-mesh sieve.

For best success in control crosses, fresh pollen is preferred over stored pollen. When fresh pollen is not available, pollen can be stored for one to several years. Pollen has been successfully stored for 15 years (Stanley, Peterson, and Mirov 1960). Desiccation for 15 minutes at 5 mm. of vacuum (Snyder 1961) or for a day over CaCl will reduce moisture content of pollen to a safe level for long-term storage. For storage, pollen should be kept in small bottles only partially filled and stoppered loosely by cotton. The temperature should be kept slightly above freezing with relative humidity approximately 20 percent.

The viability of pollen should be determined before using, because some lots store well while others do not. Pollen of fairly low percentage of germination has produced good seed set when the volume applied was varied accordingly. Pollen can be tested in distilled water with a solution of less than 0.1 percent sugar or honey (Dillon and Zobel 1957), but several other materials also are good germinating media (Echols and Mergen 1956). Estimates of percentage of pollen germination may be made after 72 hours at about 23° C. Care must be taken that turgid grains are not counted as germinated; a safe rule is to count only those in which the germination tube is longer than the width of the pollen grain, including the wings. Temperatures of about 46° C. are required for sterilization of unwanted pollen (McWilliam 1959),

but Hodgkins (1952) suggested 82° C. for 15 hours because there is variation among trees in tolerance of pollen to heat.

Four or five stages of female conelet development are recognized (Snow, Dorman, and Schopmeyer 1943; Campbell and Wakeley 1961) as an aid in controlling pollination. The stages of development dictate when pollinating bags should be put on, pollen applied, or bags removed.

Survival of cones from controlled pollination varies from very low to over 70 percent, depending on the clone, pollen used, weather, and skill of the pollinator.

Seed Handling

Loblolly pine cones ripen during October and November of the second fall after pollination. Because time of cone maturity can vary widely from year to year, the cones should be carefully observed so they can be collected when fully ripened. Wide variation in time of cone ripening also occurs among individual trees; consequently, most organizations collect by clone ripening rather than by harvesting a whole seed orchard at one time. Such variation among clones in seed production and maturity is particularly important to tree breeders because differences may be extreme. All trees of the same clone usually mature their seed about the same time, and the cones from an early-ripening clone will already have opened if collection is delayed until the average date for the orchard (Zoerb 1969).

Techniques for extraction, dewinging, drying, storage, and stratification of loblolly pine seed have been developed to a high degree and have been described in older publications such as "Planting the Southern Pines" (Wakeley 1954), the "Woody-Plant Seed Manual" (USDA Forest Service 1948), and more recently in the monograph "Loblolly Pine" (Wahlenberg 1960). Some of the older techniques have been refined and new methods substituted by workers at the Eastern Tree Seed Laboratory at Macon, Ga., or by industries or State organizations. Special attention must be given to seed from controlled pollinations because of its high value and small volume.

ASEXUAL REPRODUCTION

Vegetative propagation has been widely used in studies of loblolly pine inheritance and especially for establishment of clone banks and clonal seed orchards. Development of suitable methods of propagation has been a major part of tree breeding and research programs and has resulted in methods suitable for large-scale use under field conditions. The species has been propagated by cuttings as well as by grafts, but rooting is difficult except with cuttings from 1- or 2-year-old trees. Loblolly pine naturally

reproduces by seed and not by sprouts, root suckers, or air layers.

Rooting

In an attempt to produce genetically similar plants on their own roots, tree breeders have exhaustively tried methods of rooting, using rooted cuttings, air layers, needle bundles, and tissue culture.

In early tests with loblolly pine, good rooting was

obtained from 1-year-old seedlings, with progressively less success from older trees. All subsequent studies indicate that the effect of ortet age is strong. Studies such as those of Reines and Greene (1956-57) indicated that rooting was best for cuttings taken in December through February. In tests with trees 6 and 25 years old, successful rooting was as high as 30 percent, but later results from treatments with various concentrations of indolebutyric acid, different rooting media, and various temperatures and misting levels have been highly erratic (Grigsby 1962).

Air layering loblolly pine seedlings was fairly successful (Reines and Greene 1956-57), but air layering older trees was much more difficult (Cech 1958). There is wide variation in number and weight of roots formed among trees of the same age class, suggesting that genetic factors are involved in rooting ability (McAlpine and Jackson 1959).

Needle bundles of loblolly pine can be rooted, but it is very difficult, even with needles from young trees, to get a high percentage to root and grow into normal trees (Reines 1963; Mergen and Simpson 1964; Hare 1965; Wells and Reines 1965).

Grafting

Grafting scions from mature trees into seedling stock is the most widely used method of establishing

seed orchards of loblolly pine. Most grafting is done in the spring. Skill in grafting, control of temperature, humidity, and light as influenced by covering, and timing of graft release strongly influence success (Chase and Galle 1954; Webb 1961).

Large-scale methods of grafting loblolly pine in both the nursery bed and the field have been developed for establishing seed orchards. Scions are grafted in the spring and covered by a moisture-retaining bag; a covering supplies shade to the beds. Grafted stock can be successfully transplanted on a very large scale; mechanization has drastically cut costs of grafting in the nursery bed.

Loblolly pine scions are usually collected from large trees with a rifle. They can be shipped long distances if packed in ventilated plastic bags with dry moss and a small amount of damp moss to supply moisture (Perry and Wang 1957).

Grafting incompatibility is common (Cech 1958; Webb 1961), usually affecting about 20 percent of the clones used, of which about 7.5 percent die (Otterbach 1963). The knowledge that certain clones cannot be used in seed orchards because of incompatibility should be recognized in planning seed orchards, especially in tree selection. Grafts of loblolly pine with certain other pine species can be made, but no special benefits have been obtained (Chase and Galle 1954; Greene and Reines 1958).

VARIATION AND INHERITANCE

A knowledge of variation and inheritance of traits in each tree species is basic to development of efficient breeding plans to improve the species. Economically important traits of loblolly pine are being studied by a number of organizations, and a great deal of information is now available on inheritance, genetic gain, and seed production (Dorman 1966).

A tree species often varies among different geographic locations throughout its natural range, especially when it grows over a wide range and under varied environments. Such variation has two causes, although all of it is usually lumped under the general heading of "geographic variation." A portion of the variation occurs among stands at different locations because of environmental differences and genetic interactions with them. Other variation is a result of actual differences in genetic factors that will be expressed under different environments.

Loblolly pine occurs over a wide range of latitude and longitude which encompass different climates and which contribute to important differences in growth (Wahlenberg and Ostrom 1956).

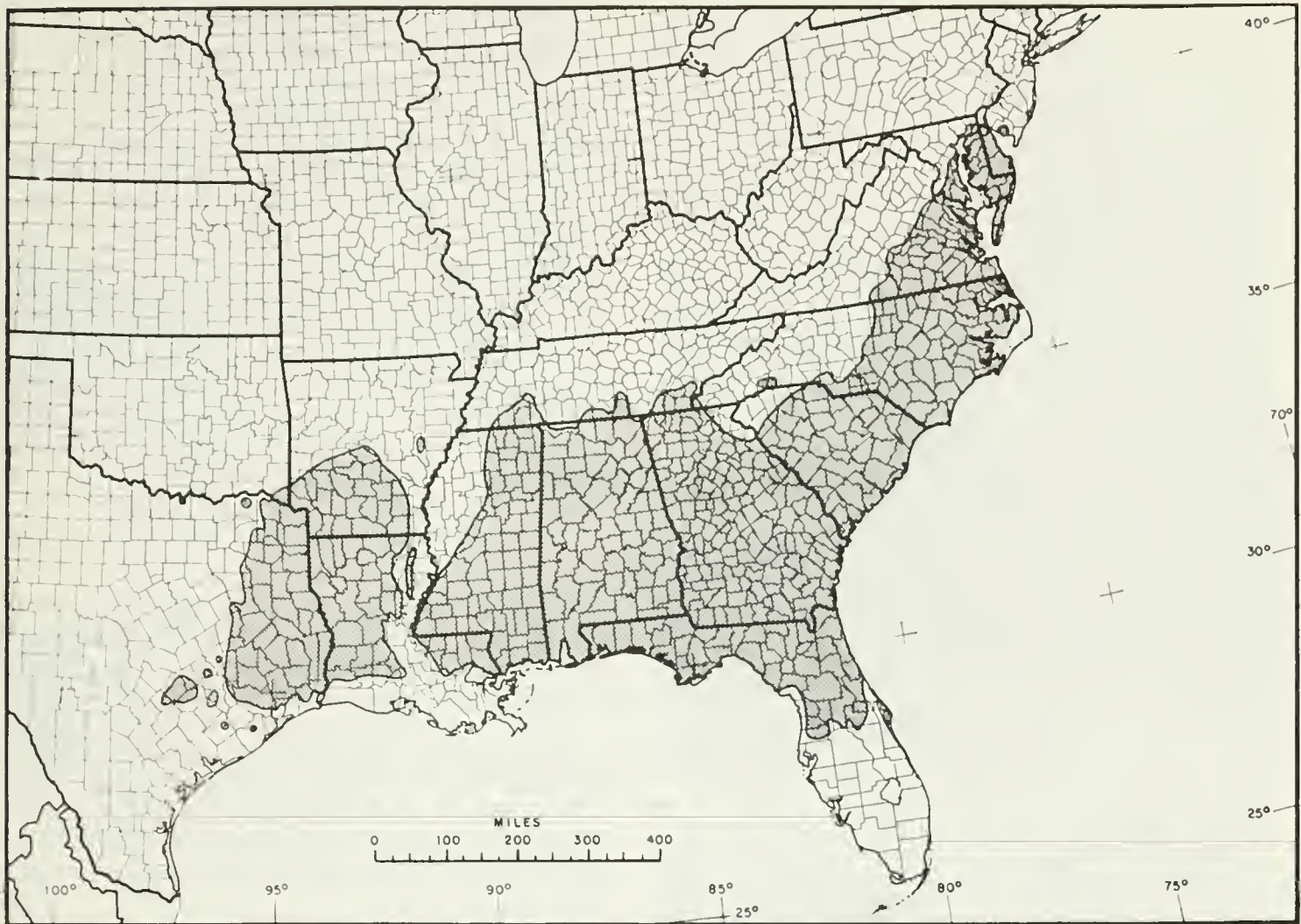
In this range, the frost-free period varies from 6 months in the north to 10 months in the south; the seasonal rainfall pattern from very wet summers and dry winters in the south to more uniform distribution

in the northeast and moderate winter rainfall but droughty summers in the northwest; the elevation from near sea level to 1,200 feet in Tennessee; and soils from low, wet sands, clays, and even peaty soils near the coasts to upland heavy clays in the Piedmont (fig. 1). The diverse environmental conditions under which this species grows have contributed to the formation of diverse geographic races. Aspects of climate that are related to distribution have been discussed (Hocker 1955).

Differences in growth and other traits attributable to location of seed source have been striking. Most plantations are young, and initial results have been reported in terms of survival, height growth, volume, and susceptibility to pests. It will be several years before the full effects of geographic source on volume yield per acre at harvest and on tree and wood quality are accurately known, but they will be considerable.

Resistance to Pests

Susceptibility to damage from insects, disease, or environmental factors is important in breeding because of the effects on seed production, growth of individual trees, and yield and quality of wood products per acre. It is of little value to produce trees



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Figure 1.—The range of loblolly pine.

with outstanding characteristics only to have them destroyed by pests or killed by cold and drought.

The most important pest of loblolly pine is fusiform rust (*Cronartium fusiforme* Hedgc. & Hunt ex Cumm.). It is highly destructive on many hundreds of thousands of acres, some of which are over 90 percent infected. Perhaps the most important finding of the genetic effort has been the degree of resistance to this disease by some parents (fig. 2). Special disease-resistant seed orchards have been established to take advantage of the early findings (Blair 1970; Zobel, Blair, and Zoerb 1971).

Of great value to applied breeding projects, progeny tests of seed orchard clones show that wide variation in rust resistance occurs among families (Woessner 1965). In a large heritability study with parental stock from a wild population, Kinloch and Stonecypher (1969) found heritabilities of rust resistance of 0.65 to 0.85, variation from 17.3 to 100 percent for infection among families, and positive correlation for resistance among parents and offspring. Variation in the pathogen has been studied, as well as variation in the host to susceptibility, and albino

forms have been described (Kais 1966). The picture as to the importance of races of rust is far from clear now, but studies now underway will help.

A good example of geographic variation is in susceptibility to fusiform rust. In loblolly pine, incidence of infection by fusiform rust is attributable to both environmental and genetic factors (Wells and Wakeley 1966). Rust infection in loblolly pines growing in eastern North Carolina is low, but the infection rate is high in North Carolina trees planted in middle Georgia, an area of high rust incidence. Incidence of rust infection is also low in east Texas loblolly pines but remains low when Texas trees are planted in middle Georgia.

High incidence of infection by fusiform rust in vigorous stands on old fields has led to fears that high growth vigor and infection rate are correlated. In studies with seedlings selected in the nursery (Barber and VanHaverbeke 1961), in one-parent progeny tests with randomly selected maternal parents (Barber 1966), and in both one- and two-parent progeny tests with seed orchard clones (Woessner 1965), infection was only weakly correlated or not related at all to



Figure 2.—Inheritance of resistance to fusiform rust in loblolly pine is fairly strong. At the top is a row of susceptible seedlings; and at the bottom is a row of more resistant seedlings growing nearby. Such differences in susceptibility have been well illustrated from the heritability study at Bainbridge, Georgia, conducted cooperatively by International Paper Co. and North Carolina State University (Kinloch and Stonecypher 1969). (Photos courtesy of Cooperative Programs, N.C. State University.)

growth rate. Extensive studies of this relationship and possible relations to cultural techniques and fertilizers are still underway.

Few definitive studies on insect resistance have been reported. Rather extensive tests in Texas and Louisiana have been made on resistance to southern pine beetles, and there appear to be resistant genotypes.

There appears to be a relationship between attack by certain insects and inherent differences among trees in rate of oleoresin flow. In a loblolly pine plantation in Tennessee, trees with a high oleoresin flow repulsed induced attacks by *lps avulsus* (Eichh.) and all trees with a measurable flow of oleoresin repulsed attacks by *lps grandicollis* (Eichh.) (Mason 1967).

Resistance to Drought and Cold

At certain locations in the western part of the loblolly pine range, rainfall is low during periods of high temperature and drought resistance has been included among desired traits in breeding programs. Droughts also occur in the deep sands in areas of heavier rainfall. Selection for increased drought resistance has been successful, as indicated by the fact that progenies of selected trees had higher survival than the controls (van Buitjtenen 1966; Gilmore 1957) and no loss in height growth (Goddard and Brown 1959; Banks 1966).

Of equal importance is developing trees to withstand cold and ice. Loblolly pine is widely planted north and inland of its natural range, where it has to withstand very cold and dry conditions during winter. Such movement has been successful when seed from northern locations are used, but trees from southern locations (central Florida, for example) freeze or their growth becomes very distorted under cold conditions. More studies of this problem are needed.

Wood Characteristics

The heavy and strong wood of loblolly pine is used for a wide range of wood products and types of paper. Studies of variation in wood and fiber characteristics have been done because of the need to maintain high and uniform quality while improving growth and yield and, if feasible, special characteristics for various products. As a basis for determining inherent differences, nondestructive techniques were developed for sampling wood characteristics in relation to tree size, age, and environmental factors. The results of these studies in techniques have been summarized (Zobel 1961, 1964) and need not be repeated.

There has been much concern about a possible change in quality of loblolly pine wood during the transition from virgin forests with old trees to man-

aged stands with much younger trees. However, in such basic characteristics as specific gravity, the range from 0.51 to 0.55 that Mohr (1897) found in trees 125 to 150 years old is about the same as that found in merchantable trees today. On the basis of samples at breast height, wood specific gravity of 1,742 trees with a mean age of 47 years averaged 0.51 and varied among individuals from 0.38 to 0.68 (Saucier and Taras 1969). Wood specific gravity of the trees selected for cloning in seed orchards because of their fast growth and good form has been the same as that of slower-growing trees used for comparison.

Wood specific gravity is considerably lower in young trees than in old ones, but wide differences are apparent among trees, as indicated by a range of 0.32 to 0.44 among 10-year-old trees in a Tennessee study of racial variation (Thor 1967). Studies too numerous to mention have reported on the effects of tree age and position within trees on wood properties.

Geographic variation.—Natural variation in wood quality has been extensively investigated because of its importance in pulp yield and quality as well as in lumber grade. Studies conducted throughout the Southeast by the USDA Forest Products Laboratory (1965), industries, and universities indicated that wood specific gravity decreases from southeast to northeast, from coast to piedmont. Differences were found to be rather large and consistent; they have a major effect on yield and pulp quality and have been important in forestry activities and land ownership patterns in this region.

In the Carolinas, wood specific gravity, percentage of summerwood, alcohol-benzene extractives, pulp yield, and zero-span tensile strength were found to be higher for trees in the Coastal Plain than for those in the Piedmont (Einspahr, Peckham, and Mathes 1964). In Maryland and Delaware, specific gravity and tracheid length were found to decrease from south to north (Whitesell, Zobel, and Roberds 1966). In the southeastern United States, differences in wood specific gravity and various types of cellulose were found, but the differences were smaller among geographic locations than among individual trees (Zobel and McElwee 1958; Zobel, Thorbjornsen, and Henson 1960).

Specific gravity and moisture content among trees in a given area usually are closely (and inversely) related. Therefore, patterns of specific gravity closely parallel patterns of moisture content. This relationship does not always hold for geographic distributions, however: Moisture contents of the loblolly pines with lower specific gravity in the mountainous area of Tennessee were found to be high as expected, but, in certain areas of the Georgia Coastal Plain, where specific gravity is high, moisture content was found to be higher than for trees in the adjoining Piedmont (Zobel, Matthias, Roberds, and Kellison 1967).

Tree-to-tree variation.—Natural variation among trees in wood specific gravity, tracheid length, and other wood morphological traits has been intensively studied in relation to growth (fig. 3). The first important paper of this type, by Zobel and Rhodes (1955), showed that wide variation in specific gravity occurs among trees, as well as within and between geographic areas, but there was a low correlation between diameter growth and specific gravity. Many additional papers have been published with similar findings. Although these cannot be cited here, they are illustrated by such papers as van Buijtenen (1963), Einspahr, van Buijtenen, and Peckham (1969), and Zobel, Kellison, and Matthias (1969). Findings from the bulk of the papers can be summarized as follows:

1. For all characteristics studied, large tree-to-tree variation is found among trees of the same age on the same site. Much of the difference has been found to be under genetic control, with narrow-sense heritabilities usually about 0.5 to 0.6.
2. Many important wood characteristics (e.g., specific gravity and tracheid length) are not highly correlated; therefore, it is possible to breed for them separately.
3. Age of tree has a major effect on wood properties, with younger trees having lower wood density, shorter tracheids, and thinner cell walls.
4. Wood qualities are affected by different environments, including fertilizer. Nitrogen fertilizers appear to have the most effect on wood of loblolly pine.
5. On older trees, growth rate and specific gravity are not highly correlated. This lack of correlation allows the development of fast-growing strains of trees either with high or low specific gravities.
6. Trees in areas with high summer rainfall and warmer climates tend to have higher wood density than those in droughty areas or cooler climates. This trend is well documented for specific gravity and other morphological characteristics of wood.
7. The pattern of wood variation, particularly the tree-to-tree differences, are such that good progress can be obtained by breeding for wood quality.

In an important paper, Barefoot, Hitchings, and Ellwood (1964) reported on the strong relationship of wood characteristics of four selected loblolly pines to kraft paper properties. Several such studies have been made to help the tree breeder know how much effort should be expended to improve wood quality characteristics. The most important morphological characteristic of wood for most pulp and paper products is thickness of the cell walls (estimated by specific gravity); second in importance is tracheid length, especially for tearing strength.



Figure 3.—Improved forests are going to be fast-growing. If proper care is taken, they can be both fast-grown and satisfactory in wood quality. Shown in cross section are a fast-grown, improved loblolly pine with relatively high specific gravity (left) and a normally grown loblolly pine from the woods with average specific gravity (right). With selective breeding, trees can be “tailor made” with desired qualities. (Photo courtesy of Cooperative Programs, N.C. State University.)

Many studies have been made on the inheritance of wood qualities *per se* and their relationship to other desired characteristics. Progeny tests of seed orchard clones have shown differences in yields caused by different growth rates combined with different wood specific gravities, and it was concluded that breeding for both traits is highly desirable (Zobel *et al.* 1969).

In addition to specific gravity, genetic studies of

numerous other wood characteristics have been made. Greene (1966) found that heritability of tracheid length based on a regression of progeny on mid-parent was 35 percent. Fiber angle in tracheids was found to be under genetic control (Jackson and Morse 1965).

In 5-year-old trees, compression wood had a heritability of 0.95, specific gravity 0.73, and volume growth 0.23 (Shelbourne, Zobel, and Stonecypher

1969). Compression wood showed a low positive correlation with tree height, diameter, and volume and a low negative correlation with specific gravity. Significant differences were found in spiral grain in 4-year-old control-pollinated families, and it was concluded that genetic variation was of the non-additive type (Zobel, Stonecypher, and Browne 1967).

Differences in holocellulose yields among trees of the same age growing on the same site at the same rate varied widely, and family means of offspring varied from 83.8 to 85.0 percent. Intra-family variability was so high that the differences were not found to be statistically significant in a preliminary study (Zobel, Stonecypher, Browne, and Kellison 1966). For young trees, only a small additive component for cellulose yield *per se* was found, indicating that a selection program would be of limited value.

Growth Rate

The universal characteristic included in breeding programs is growth rate. This complex characteristic

is most difficult to work with, especially since juvenile growth is not always indicative of mature growth. The arbitrary rule many breeders follow is to assess growth at one-half rotation age.

The inheritance of the height component of growth appears to be moderately strong, but the diameter component, at least on older trees, is weakly inherited. Complicating the picture are physiological, adaptive, and disease problems that cannot easily be taken into account in breeding for growth improvement.

Loblolly pine is a fast-growing species (fig. 4). On 1 acre of a private 30-acre plantation of loblolly pine on Wadmalaw Island, S.C., the 639 trees had 192.6 square feet of basal area and a volume of 48.29 cords at age 11 (Langdon, Hatchell, and LeGrande 1970). All trees averaged 7.5 inches in diameter, and dominants and codominants averaged 54 feet in height. There were 130 trees 9 inches or larger in diameter. Two trees were 11 inches in diameter, and one of them was 59 feet tall.

Racial variation.—Exhaustive studies have been made on the effect of seed source on growth. In the oldest such study in the South, near Bogalusa, Loui-



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Figure 4.—Portion of 30-acre private plantation of loblolly pine in South Carolina. The 11-year-old tree being measured was 11 inches d.b.h. and 55 feet tall.

siana, loblolly pines from Livingston Parish near Baton Rouge produced 78 rough cords per acre at 35 years of age, those from Texas produced 32 cords, those from Georgia produced 34 cords, and those from Arkansas produced 13 cords (Wakeley and Ber-caw 1965). Wood yield was influenced by differences in growth, survival, and resistance to fusiform rust. The Georgia source was the most heavily infected of the four.

At ages 5, 10, and 15 years, the range-wide study sponsored by the Forest Tree Improvement Committee showed strong clinal variation in growth, with trees from coastal areas generally growing faster than those from inland areas in all but the coldest planting locations (Wakeley 1961; Wells and Wakeley 1966; Wells 1969). When trees were moved from one extremity of the range to another, they produced less than one-half the volume of local seed because of a combination of poor survival and slow growth; but when trees of coastal origin were moved inland as far as 225 miles in the southern part of the range, they grew faster than trees that originated in inland areas.

Four of the 15 sources of loblolly pine in this range-wide study had considerably less fusiform rust than the others. These relatively resistant trees were those originating west of the Mississippi River, in Livingston Parish, Louisiana, and on the eastern shore of Maryland. Another range-wide study of 36 seed sources grown at Crossett, Arkansas, also demonstrates the fast growth potential of loblolly pines from coastal areas, especially that of trees from the Carolinas (Grigsby 1973).

The results of the range-wide studies have been corroborated and expanded upon by studies in which intensive samples were made of loblolly pines throughout Georgia (Kraus 1967), Alabama (Goggans, Lynch, and Garin 1972), Mississippi (Wells and Switzer 1971), and North Carolina (Lantz and Hofmann 1969). A study of several populations of loblolly pine from Louisiana that were planted elsewhere in the same State revealed that those from Livingston Parish and western Louisiana were resistant to rust, but differences in height between northern and southern Louisiana sources, while suggestive, were not statistically significant (Crow 1964; Merrifield 1965).

A number of smaller studies have indicated that racial differences in survival, height growth, and resistance to pests or drought exist in Texas (Zobel and Goddard 1955; Goddard and Brown 1959; Youngman 1967) and Mississippi (Thames 1962, 1963; Wells 1966).

The within-State studies have established that, in addition to the patterns of variation established by the range-wide studies, loblolly pine varies clinally in survival potential and resistance to fusiform rust. Loblolly pines from the Gulf and the South Atlantic Coasts survive planting slightly less well and have less inherent resistance to rust than do those from inland areas.

Wells (1969) has suggested that zones of seed collection and planting be established that are designed to take advantage of these inherent geographic variations in rust resistance and in potential for growth and survival. He further suggests that throughout the 1970's, while seed orchards are coming into full production, geographic variation should be more fully utilized as a source of genetic gain. The greatest single gain could probably be made by using the rust-resistant, fast-growing loblolly pines from Livingston Parish, Louisiana, throughout the southern two-thirds of Mississippi, Alabama, and Georgia, wherever sites are suitable for loblolly pine. In the Carolinas, loblolly pines should not be transferred between the Piedmont and the Coastal Plain. For plantings near or north of the northern boundary of the natural range, only loblolly pines from near this northern boundary should be used because of their better survival, growth, and resistance to snow and ice damage, as shown by tests in Maryland (Little 1969), Virginia (Kormanik, Haney, and Dorman 1961), southern Illinois (Woerheide 1959), Tennessee (Thor and Brown 1962; Thor 1967), Arkansas (Maple 1966), and throughout the Tennessee River Valley (Zarger 1961). In a test in eastern Tennessee, Thor (1967) found that trees originating in the North Carolina Piedmont produced 8.91 tons of extracted wood per acre whereas those originating in the Piedmont of north Georgia produced only 5.3 tons. This difference was largely due to differences in volume growth, because extracted specific gravity of the North Carolina source (0.374) differed little from that of the north Georgia source (0.372).

Tree-to-tree variation.—Progeny tests of parents with different traits or selected at random have consistently shown large differences in growth attributable to parentage. In a one-parent progeny test with 105 maternal parents, the 5-year height of the 10 progenies making the slowest growth was 5.6 feet and that of the 10 progenies making the fastest growth was 7.6 feet—or 36 percent more height growth (Minckler 1942). Significant differences of 10 to 20 percent in height growth at 3 years of age occurred among progenies of trees that had been chosen for differences in stem form (Perry 1960). Narrow-sense heritability of diameter growth was computed to be 0.35 for 2-year-old seedlings and 0.14 for 3-year-old seedlings (Stonecypher, Cech, and Zobel 1964). When progeny of 11 trees selected in southeast, central, and northwest Georgia were planted in central Georgia, the fastest-growing family from each of the three areas had a height superiority over the slowest-growing family of 17 to 31 percent after five growing seasons (Barber 1966). The slowest-growing family of the slowest-growing seed source averaged 8.4 feet, and the fastest-growing family of the fastest-growing seed source averaged 12.0 feet—or nearly 43 percent greater height, indicating that the effects of racial selection and plus-tree selections may be additive.

Maternal parents selected for good growth rate and other desirable traits have, in general, produced highly vigorous offspring. In Texas, progeny of four out of six maternal parents selected for good characteristics were significantly better in most traits than the controls, and two progenies were significantly taller than the controls (Goddard, Brown, and Campbell 1959). In Texas, growth of progenies of loblolly pine parents in seed production areas has been, on the average, about the same as that of the controls, but these progenies have been more uniform and there have been wide differences among individual families in growth (van Buijtenen 1969). The 10 highest-producing families yielded 1.82 cords per acre per year, the controls yielded 1.54 cords, and the 10 lowest-producing families yielded 1.14 cords. The lowest growth of an individual family was 0.90 cord per acre per year, and the highest growth of an individual family was 2.05 cords. Large differences in yield of dry wood per acre occurred in open-pollinated families of certain parental trees selected for industrial seed orchards (Zobel *et al.* 1969). Yield varied from 1.8 to 2.7 tons of dry wood per acre per year among 7-year-old families growing on an excellent site. In general, growth of progenies from rogued seed orchards is expected to be about 10 to 20 percent higher than that of commercial planting stock.

Although the results of most progeny tests are based on the performance of young trees, such tests have revealed large differences among control-pollinated families. In Georgia, comparison of progeny growth from open-, control-, and self-pollinations showed that both general and specific combining abilities are important in loblolly pine (Greene, Porterfield, and Carmon 1964). As female parents, some trees combined well with certain males but not others; selfing caused reduced growth rate in progeny of certain trees but not in others. However, in a large study made with unselected parents in Georgia, narrow-sense heritability was only 0.12 for first-year height growth and 0.10 for second-year height growth (Stonecypher 1966).

In progeny tests of clones in certain industrial seed orchards, the mean heights of control-pollinated families were greater than the mean height of commercial checks and the most vigorous cross produced 28 percent more volume than the controls by the fourth year (Woessner 1965). When six males were crossed with the same female, wood yield of the resulting families at 7.5 years old varied from 1.5 to 2.8 tons per acre per year on the basis of equal numbers of trees per acre (Zobel *et al.* 1969). In Georgia, the best F_1 cross for height growth and wood yield produced the fastest-growing F_2 progeny when measured at 2 years of age (Greene 1969). The range in height of 2-year-old F_2 families of 3- or 4-year-old parents was 6.6 to 9.1 feet, and there was a wide range in height within families.

In the industrial programs, second-generation selections are now underway (fig. 5). Emphasis is on im-



Figure 5.—Breeding of loblolly pine has proceeded into advanced generations. Shown is a 5-year-old second-generation selection from progeny tests conducted by Union Camp Corporation in Georgia. Such trees are highly superior to the plantation averages and represent the very best trees of the best families. (Photo courtesy of Cooperative Programs, N.C. State University.)

provement of growth rate by obtaining the best trees of the best families. The initial second-generation selections are 40 to over 80 percent faster-growing than plantation averages, even though only straight-boled, small-limbed trees were selected.

Investigation of physiological and chemical differences among trees and progeny has been one method of studying the genetics of growth. A study in North Carolina (Ledig and Perry 1969) in which a threefold difference occurred among control-pollinated progenies in dry-weight growth in one season showed that the seasonal pattern of photosynthetic rate varied also. This variation could explain why measurement of photosynthetic rate at one period in the growing season might not show differences among progenies or a correlation of photosynthetic rate and growth, as was observed in an earlier study (Burkhalter, Robertson, and Reines 1967).

The better growth and survival of loblolly pine seedlings in the higher nursery grades than in the smaller size grades has encouraged tree breeders to select super or outstanding seedlings in nursery beds in order to isolate superior trees. This approach to selection has been productive but not highly definitive. In Texas, the plus-seedlings were 25 percent taller at 5

years than average control seedlings (Zobel, Goddard, and Cech 1957). In Tennessee, 68 percent of the plus-seedlings were taller after 10 years than the average control trees, but they suffered the same kind and amount of damage from snow (Zarger 1965). In Georgia, plus-seedlings had 25 percent greater volume after 9 years than the controls, but they had the same amount of infection by rust (Hunt 1967). In South Carolina, 10-year-old plus-seedlings were about 30 percent taller than the controls (Langdon, Hatchell, and LeGrande 1968). Thus, selection in nursery beds was partially effective for height growth but did not produce consistent gains in other important traits, and often the fast-growing nursery selections had wolf-tree characteristics.

In summary, even though growth is a complex characteristic, it has responded better in loblolly pine to genetic manipulation than originally expected. Most breeders now are certain of 10 to 20 percent improvement over commercial checks in merchantable stands after moderate selection. Some families are 100 percent better than the commercial checks, but some selected trees produce progenies with inferior growth. It is clear that, if maximum improvement of growth rate is to be obtained, such improvement must combine phenotypic with family (progeny-test) selection. Second-generation improvement in growth is expected to be considerable, and second-generation selection and breeding will soon show the gains to be obtained in growth following very intensive selection from uniform stands.

Tree Form

Many individual traits influence the shape and size of tree stems, crowns, and branches, and probably most of them are inherited independently. Stem straightness and forking are very important for products such as poles and lumber and also affect pulp quality, whereas other traits such as branch angle or size are less important unless they are extreme.

Improvement in tree form is one of the important objectives in breeding loblolly pine because crooked stems, poor natural pruning, numerous branches, and large crowns are common minus traits of this highly vigorous species (Southeastern Forest Experiment Station 1962). Environmental factors, particularly growing space, influence branch and crown size, but loblolly pine trees in the relatively uniform environment of a planted stand differ from each other and these differences may be inherent (fig. 4). Trees with slender crowns and small branches do occur, however, and grafted clones of these trees in seed orchards are very uniform (fig. 6). Differences among grafted clones are apparent, even at an early age; Brown (1968) found that heritabilities for branch and growth traits were in the order of 70 to 80 percent at the end of the second year.

Large differences in stem and crown form occur in

progeny tests. Heritability of crown width in 7-year-old open-pollinated progeny of trees with well-formed crowns and of trees with poorly formed crowns was 34 percent (Trousdel, Dorman, and Squillace 1963). In Texas, the ratio of mean limb length to tree height was significantly lower in progeny of three out of five trees selected for good quality than in check trees, but there were no significant differences in mean limb angles (Goddard *et al.* 1959).

Controlled pollinations were made among crooked loblolly pine trees in Florida, and the progeny were compared with those of straight trees (Perry 1960). At 2 years of age, progenies from crosses between straight trees contained four times as many straight seedlings as did progeny from crosses among crooked parents. At age 7, about the same proportion of crooked and straight trees existed (Goddard and Strickland 1964). It was concluded that there were reasonably strong general and specific combining abilities for stem straightness.

Several recent publications have shown the strength of inheritance of bole straightness. Older progeny tests indicate that enough straightness has been achieved in one generation of selection so that further emphasis on this characteristic is unnecessary. Intensive studies on how to measure this characteristic and its inheritance (Shelbourne and Namkoong 1966; Shelbourne 1967) have been made. It has been found that a subjective rating scheme is nearly as successful in categorizing tree straightness as is accurate measurement. The importance of tree form in pulp yield and quality is now being tested by pulping crooked, large-limbed families and straight, small-limbed families. Effects are evident but do not appear to be large.

Because emphasis on volume improvement involves the tree breeder with the inherent difficulties of selection from wild stands, most breeders working with loblolly pine have emphasized quality improvement more than growth improvement in the first generation. Despite this emphasis, considerable increase in growth rate has been obtained. In future generations of breeding, emphasis on volume will be much greater.

Correlation Among Traits

Important characteristics may be correlated negatively, positively, or combined at random. If correlated positively, an improvement in one will automatically result in an improvement in the other; if correlated negatively, an improvement in one will result in a decrease in the other; if there is no correlation, improvement of one trait will not change another. As of now, no economically important traits of loblolly pine are so negatively correlated that progress in breeding is badly impeded.

If care is taken in breeding, increased growth rate need not lower wood specific gravity, increase susceptibility to fusiform rust or drought, or change crown and stem form. Because most traits are not strongly



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Figure 6.—This grafted clone of loblolly pine has the good stem and crown characteristics for which the ortet was selected. Individual ramets of the same clone (shown here at 5 years of age) vary little in economically important traits.

correlated, all important traits must be considered and at least held at present levels when choosing breeding stock or seed orchard clones. Otherwise, there will be no overall improvement and the performance of some traits may even be lowered. In loblolly pine, improvement of several major traits at the same time is the most complex and important problem facing the tree breeder.

Loblolly pine varies in many important traits, and trees that are superior in some traits but decidedly inferior in many others are unuseable in seed orchards. Thus, tree breeders are unable to capitalize on the theoretically advantageous practice of making the greatest genetic gain by selecting for one or a very few traits at one time. For example, if plus-trees are selected for seed orchards only on the basis of stem volume, stem straightness, and resistance to fusiform rust, these selections might include trees unmerchant-

able because of poor branch form, natural pruning, stem forking, or wood properties. Furthermore, such trees might be unsuitable because of poor flowering characteristics, graft incompatibility, and poor combining ability with other clones.

Tree growth and quality are largely influenced by qualitative characteristics which are important when evaluating correlations among traits. For example, if ring width and wood specific gravity are negatively correlated but the regression coefficient is very low, then trees strongly selected for both wide rings and high specific gravity will have offspring with above-average wood specific gravity as well as growth rate.

All plant breeders working with loblolly pine must be alert to possible correlations among traits. Several papers now in press will clarify these relationships somewhat—luckily, most important traits have not been found to be negatively correlated.

Mutations

In studies of techniques for inducing mutations, Mergen (1959) treated male strobili of loblolly pine during meiotic and post-meiotic divisions; Pedigo (1960) irradiated seedlings of different ages; Snyder,

Grigsby, and Hidalgo (1961) treated seed at various moisture contents; and Davis (1962) treated seed and seedlings with different dosages of cobalt-60 gamma radiation. Mixoploid and polyploid seedlings occur infrequently in seed beds; the resulting plants are low in vigor and usually do not mature.

INTERSPECIFIC HYBRIDS

The major southern pines and certain minor species are closely related and many of them hybridize naturally; this hybridization contributes to variation among geographic areas. Artificial hybrids of some species are also under study.

Natural Hybrids

The hybrid of longleaf (*Pinus palustris* Mill.) and loblolly pines, Sonderegger pine (*Pinus x sondereggeri* H.H. Chapm.), was probably the first pine hybrid recognized (Chapman 1922), and seedlots of longleaf pine may contain 0.5 to as much as 15 percent hybrid seed. Evidence of at least three generations of hybridization of longleaf and loblolly pines with intermediate forms was found in a natural stand in Louisiana (Namkoong 1966). In Texas, progenies of Sonderegger pine were considered unsatisfactory because of slow growth, poor stem form, and large limbs that broke readily in ice and windstorms (van Buijtenen 1969).

The existence of trees intermediate between loblolly and shortleaf (*Pinus echinata* Mill.) pines in morphological traits (Zobel 1953) and electrophoretic patterns of seed proteins (Hare and Switzer 1969) indicate that this hybrid occurs in Texas. In Mississippi, trees with traits similar to those in artificial hybrids of loblolly and shortleaf pines were found at two locations (Mergen, Stairs, and Snyder 1965). Those who work closely with loblolly pine find hybrids occurring throughout its natural range. Nearly every seed orchard has a hybrid of some type within it. These include hybrids with longleaf, shortleaf, pond (*P. serotina* Michx.), slash (*P. elliottii* Engelm.), and pitch (*P. rigida* Mill.) pines. Recent studies (Little,

Little, and Doolittle 1967; Smouse 1970) have confirmed the existence of these hybrids and have attempted to delineate their patterns of occurrence.

Artificial Hybrids

Loblolly pines have been crossed with several other southern pine species (Critchfield and Little 1966), and descriptions have been given (Little and Righter 1965; Little *et al.* 1967; Schmitt 1968).

In Korea, extensive use in forestry has been made of a cross of loblolly pine with pitch pine, and back crosses are being studied (Hyun 1958; Hyun, Koo, and Ahn 1965). For that location, the hybrids have some of the form and growth characteristics of loblolly pine and the cold resistance of pitch pine. Hybrids between New Jersey loblolly and Pennsylvania pitch pines showed high resistance to cold damage (Hyun 1970).

Crosses of loblolly pine with other pines have not shown much promise, largely because of the large number of economically important traits involved and the difficulties of seed production, but results with carefully chosen maternal and paternal parents might be better (Schmitt 1968). Plantings in submarginal areas (too dry, too wet) have shown that some hybrids may be useful. They may also be of value in extending the range northward; crosses of slash x shortleaf or loblolly x shortleaf have shown some good traits. In areas of high infection by fusiform rust, the loblolly x shortleaf hybrid shows real promise because of its nearly complete resistance to the disease and reasonably good growth characteristics.

Seed yield per cone in species crosses involving loblolly pine are lower than in crosses within species (Snyder and Squillace 1966).

IMPROVEMENT PROGRAMS

If genetically improved trees are to be used, tree improvement programs must be geared to the utilization of the species and to opportunities presented by the existence of large tree planting programs. Loblolly pine is ideal for a wide variety of forest products, and it will grow under many different environments. It is now the most commonly planted species in the Southeast. Many forest industries are breeding strains for their own use, and public agencies are developing trees for landowners in general.

Estimates of the cost-benefit ratios in tree improvement show that the investment is sound (Marler 1963; Davis 1967). Tree improvement programs are no longer considered to be research by the major industries who now include these programs as a regular part of their forest management activities. By about 1978, nearly all loblolly pine, whether from industry, State, or Federal nurseries, will be from seed orchard stock. The basic methods of tree breeding with their important features have been described (Dorman

1962; Cech 1963). Because most work in the applied breeding of loblolly pine is combined with production of commercial amounts of seed in seed orchards, various combinations of breeding methods are used (fig. 7). Seed from a clonal orchard represents the result of racial selection, plus-tree selection, roguing based on progeny tests, and natural mating among the best clones. The theory and methodology of seed orchards as applied to this species have been discussed (Zobel and McElwee 1964).

Most activities deal with selection, either by phenotype or through progeny testing. More sophisticated methods such as species hybridization, haploid breeding, mutation breeding, and polyploid breeding are used either on a very small scale or are still in the experimental stage. Advantages and disadvantages of various breeding methods have been discussed (Dorman 1962; Cech 1963); some of these methods have serious limitations for use with loblolly pine.

Selection

Loblolly pine is a variable species with several traits showing continuous or discontinuous variation with geographic location. Differences are so great that separate seed orchards are necessary to produce seed for specific areas and products. Because of geographic differences, it is not possible to use seed of one race for planting in all other areas of the natural range or in all foreign countries. Stands of the proper race can now be partially selected on the basis of the results of current studies (Wells 1969). The recommended zones of seed collection may change as studies mature and new studies indicate boundary locations and seed

movement more precisely, but good guides are now available. Local seed has been used as a standard in planting, but current studies show that there are certain geographic locations in which distant sources will sometimes perform better than the local race.

Within local geographic areas, phenotypic growth rate, tree form, and wood quality vary from stand to stand. Regardless of whether individual trees are to be used for breeding stock or for clonal seed orchards, maximum pressure should be exerted in selecting the best individual tree in the best stand of the best race. A large number of trees for clonal orchards should not be selected from a single stand. The history of the development of many loblolly pine stands from old fields with only one or very few trees as parents indicates that inbreeding could quickly become a problem. If trees from such stands are crossed, inbreeding will result. Because of this tendency for relatedness within stands, some of the good growth response from seed orchards may have resulted from bringing together individuals from unrelated matings so they could outcross in the seed orchard.

Guides for selection have been prepared by a number of individuals and organizations. Although selection criteria or tree rating schemes may vary, they all identify similar trees of superior phenotypic characteristics (Cech 1959). Because the objective in selecting trees for clonal orchards is to define parental trees that will produce progeny of the highest possible overall performance, trees with a good combination of good traits are desired rather than trees whose progeny show improvement in only one trait. Working with several characteristics is difficult but possible because there is large tree-to-tree variability in the natural stands from which selections are made. Selec-



Figure 7.—Kimberly-Clark Corporation's facilities for mass production of genetically improved seed in Alabama include nursery beds (foreground), a seed orchard of loblolly pine (behind the beds), and seed orchards of other pines and hardwoods and progeny test plots (to the right and rear).

(Photo courtesy of Kimberly-Clark Corporation.)

tion should be concentrated on economically important traits with a high heritability; basic data on which to make decisions are now becoming available and selection methods are improving. Selection for certain traits is possible in the seedling stage; straightness of bole can be accurately estimated at 5 years; and other traits such as growth rate or volume growth cannot be determined with certainty before one-half rotation age.

Selection Criteria

Form.—Although loblolly pine is a species with poor form, great improvements in various categories of form have been made through the applied breeding programs. Crooked trees in plantations can largely be avoided by using only straight trees with little taper as parents. The species tends to have very large limbs with resultant large knots; selection for fine crowns has been partially successful. Progeny tests indicate that control of ramicorn branching and forking is partially genetic and that the tendency toward ramicorn branching is very strong in progenies from certain parents. The genetics of forking has not been determined, but it occurs consistently. If this trait proves to be under sufficient genetic control, it will present few obstacles to selection.

Trees with good natural pruning are preferred, and progenies differ considerably in this characteristic. Crown efficiency, as expressed by the relation of volume growth to crown size, should be high. Some very efficient parental trees have been found.

Growth rate.—Major emphasis in selection should be given to traits of the individual tree that contribute to volume growth per acre. Only the dominant trees in a stand should be considered for selection; selection is most efficient if carried out in regularly spaced, even-aged stands. Traits such as resistance to drought, resistance to transplanting shock, photosynthetic efficiency, shade tolerance, and perhaps others influence volume growth per acre as well as growth of individual trees, and they can best be evaluated in progeny tests.

In loblolly pine, growth rate among trees in wild stands is highly variable. If the proper breeding method is used, it is rarely necessary to sacrifice growth superiority when selecting for tree form or wood quality. Trees with combinations of the several traits that affect growth form and adaptability are not common, but they can be found by a systematic search. As has been pointed out by Zobel *et al.* (1969), it is more effective to increase wood weight yields by increasing both volume growth and specific gravity than by concentrating on a single characteristic.

Flowering ability.—Age at which flowering begins in young trees or grafts and the timing and volume of flowering in seed orchards are important traits. These are difficult to evaluate in selection, but they cannot be ignored. Relationships between flowering of the mother tree in a dense stand and in a fertilized seed

orchard where the trees are open-grown often are not close. Differences in flowering among clones are considerable, but some variation can be tolerated, depending on administrative objectives and seed orchard management. In highly refined breeding programs to create new strains through sustained breeding over several generations, flowering at an early age is highly advantageous—provided that economically important traits in progeny can also be adequately evaluated for each generation.

Pest resistance.—Selection for resistance to fusiform rust is important in loblolly pine in order to maintain good quality in stem form and improve volume production per acre. Variation is large, heritability is good, and progress is rapid in breeding for resistance (Blair 1970; Zobel, Blair, and Zoerb 1971). Racial selection, as well as plus-tree selection within races, is important in improving resistance.

Stem defects from rust galls are very common. These degrade trees and lower growth rate per acre. Wood from the infected portion of the stem is abnormal and produces poor end products. If stands are available, selection for resistance to rust should be undertaken where incidence of infection is high. Phenotypic selection for rust resistance alone is only partially successful; however, combined with progeny tests, it has proved to be very successful (Blair 1970).

Young loblolly pines suffer damage from tip moths. Ubiquitous attacks in the lower crown and stem affect form quality and may affect growth. Single-tree and racial selection appear to be largely ineffective, but selection among natural or artificial interspecific hybrids with resistant parental species might be effective.

Selection for resistance to drought or other environmental factors, such as snow breakage or deep, peaty, acidic soils, etc., is profitable at specific geographic locations.

Wood qualities.—Because weight of wood, as reflected by specific gravity, affects strength, yield, and quality factors lumped together under wood quality, selection practices must be based on product requirements. Wood specific gravity has low correlation with growth rate, but it cannot be ignored in selecting for fast growth because of the wide range in wood weight among fast-growing trees.

Selection for high specific gravity increases yield of pulp per unit of wood volume and, additionally, affects qualities important in paper pulp (van Buijtenen 1964). Quality characteristics of pulps must be considered as well as yield. For certain paper products, low-gravity wood is preferred. Loblolly pine has been selected for high, average, or low specific gravity in various breeding projects, depending on the end product sought.

Length of fiber in loblolly pine is under genetic control and could be manipulated by selection if such proves desirable. This problem should be carefully considered before extensive work is undertaken

because of the high cost of sampling parents and progeny. It is commonly stated by mill managers that fiber length is of key importance in paper manufacture, but exhaustive tests (Barefoot *et al.* 1964) indicate that wall thickness of summerwood is most important. This characteristic can be easily changed by breeding for specific gravity.

Seed Production Areas

For large-scale planting, management of carefully selected and treated stands for seed procurement is superior to purchasing seed on the open market. Seed production areas are considered as intermediate stages of a seed improvement program until seed orchards are productive (Cole 1963; Easley 1954).

Seed production areas are often desirable from an administrative as well as a genetic standpoint. Administratively, seed procurement is more orderly; genetically, the seed produced is the result of intensive selection of proper race, moderate selection for form and pest resistance, and fairly low selection for vigor, growth rate, and wood quality. Volume improvements have been low from seed production areas, but form has responded better. The greatest value of a seed production area is the assurance that the proper geographic source has been used.

Seed Orchards

As a species, loblolly pine is well suited to the development of genetically improved planting stock by combining several methods of breeding with seed production on a commercial scale. For tree vigor and quality and other individual traits of importance, strong selection applied to the proper race is essential. If the crossing patterns and progeny tests are properly designed, combining ability based on results of progeny testing can be effectively used for first- or later-generation orchards.

Publications are available on the theory and establishment of seed orchards. Standards for the certification of seed, if so desired, are available in handbooks of certain crop improvement associations.

A seed orchard is not an end in itself. It may be modified, expanded, or replaced according to the administrative and technical requirements of producing large amounts of high-quality seed on a rigid time schedule. In order to have continued progress, seed orchards for both research and production are needed. Great care must be taken so that the breeder does not work himself into a "dead end" after a generation or two because of inbreeding resulting from poorly designed crossing patterns. As the value of the strains created by intensive breeding increases, the design and culture of seed orchards will become more complex

and economically rewarding.

Seed orchards to replace those now in use should be designed on the basis of the best information available. The physical characteristics of the orchard, such as size, number of clones, tree spacing, culture, and protection, can be determined on the basis of experience gained to date. The clonal or seedling stock planted should be selected or created through crossing to produce seed with the genetic qualities desired. Most of the clones or breeding stock should be chosen on the basis of performance tests.

It may not be possible to combine creative breeding with commercial seed production as is being done in current or first-generation seed orchards. Rather, it may be necessary to create improved stock elsewhere and leave only the last cross to take place among seed orchard clones and produce seed in large volume. The methods by which new strains are created and the combination of traits they have are almost too numerous to mention.

Each seed orchard will require a high level of technical planning appropriate for the objective. Seed orchards consisting of plant material hauled in out of the woods and planted no longer suffice. There is no simple rule of thumb for establishing the perfect seed orchard.

There should be a broad spectrum of genes available from the research orchards. From these, parental material for production orchards will be so chosen that certain characteristics such as fast growth, straight stems, and disease resistance will be narrowed but adaptability will be enhanced. We are starting with a broad adaptability, and this should easily be maintained. However, for certain special conditions, such as severe disease infection, orchards with a very narrow base will be developed to overcome the problem encountered. These will be second-generation orchards made up of just two clones that are based on specific combining ability, and such clones will not be used as a main basis for further breeding. The latter will be done in the research orchards.

Most production orchards are essentially designed to fulfill a particular need at a particular point in time. The second-generation material can lead to related matings even with the best of designs and an initial base of several hundred clones. To avoid such matings, an open system into which new genes are constantly infused will be used, rather than the closed system which results in faster gains but has the problem of an insufficiently large genetic base. Already, crossing among second-generation selections is taking place in preparation for the third phase. In such work, it is essential to plan far ahead so that the program does not ultimately founder because of an undesirably narrow genetic base.

LITERATURE CITED

- Banks, P.F.
1966. Early height growth in Rhodesia of progenies of *P. taeda* from Texas. *Rhod. Zambia Mal. J. Agric. Res.* 4: 3-7.
- Barber, John C.
1966. Variation among half-sib families from three loblolly pine stands in Georgia. *Ga. For. Res. Council. Res. Pap.* 37, 5 p.
——— and David F. VanHaverbeke.
1961. Growth of outstanding nursery seedlings of *Pinus elliottii* Engelm. and *P. taeda* L. *USDA For. Serv. Southeast. For. Exp. Stn. Pap.* 126, 12 p.
- Barefoot, A.C., R.G. Hitchings and E.L. Ellwood.
1964. Wood characteristics and kraft paper properties of four selected loblolly pines. I. Effect of fiber morphology under identical cooking conditions. *Tappi* 47: 343-356.
- Bergman, Axel.
1968. Variation in flowering and its effects on seed costs: A study in seed orchards of loblolly pine. *N. C. State Univ. Tech. Rep.* 38, 63 p.
- Blair, Roger L.
1970. Quantitative inheritance of resistance to fusiform rust in loblolly pine. *Ph.D. Thesis, N. C. State Univ.* 73 p.
- Brown, Edward F.
1968. Clonal variation in seed orchards. *M.S. Thesis, Univ. Ga.* 30 p.
- Burkhalter, Alva P., C. Frank Robertson and M. Reines.
1967. Variation in photosynthesis and respiration in southern pines. *Ga. For. Res. Council. Res. Pap.* 46, 5 p.
- Burley, Jeffrey.
1967. Review of variation in slash pine (*Pinus elliottii* Engelm.) and loblolly pine (*P. taeda* L.) in relation to provenance research. *Res. Commonw. For. Rev.* 45(4), No. 126: 322-338.
- Campbell, T.E., and Phillip C. Wakeley.
1961. Possible refinements in controlled pollination of southern pines. *Sixth South. Conf. For. Tree Improv. Proc.* 1961: 121-128.
- Cech, Franklin C.
1958. The vegetative propagation of *Pinus taeda* L. (loblolly pine). *Ph.D. Thesis, Agric. & Mech. Coll. Tex.*
1959. Superior tree selection—a comparison of grading systems. *Fifth South. Conf. For. Tree Improv. Proc.* 1959: 49-52.
1963. Breeding methods in tree improvement. *Seventh South. Conf. For. Tree Improv. Proc.* 1963: 27-30.
- Chapman, H.H.
1922. A new hybrid pine (*Pinus palustris* x *Pinus taeda*). *J. For.* 20: 729-734.
- Chase, Spencer B., and F.C. Galle.
1954. Pine grafting—a preliminary report. *Tenn. Val. Auth. Tech. Note* 18, 6 p.
- Cole, Donald E.
1963. Management of pine seed production areas. *Seventh South. Conf. For. Tree Improv. Proc.* 1963: 44-49.
- Critchfield, William B., and Elbert L. Little, Jr.
1966. Geographic distribution of the pines of the world. *USDA For. Serv. Misc. Publ.* 991, 97 p.
- Crow, A.B.
1964. Ten-year results from a local geographic seed source study of loblolly pine in southeastern Louisiana. *La. State Univ. and A&M Coll. Sch. For. & Wildl. Manage., L.S.U. For. Note* 57, 4 p.
- Cumming, W.C., and F.I. Righter.
1948. Methods used to control pollination of pines in the Sierra Nevada of California. *U.S. Dep. Agric. Circ.* 792, 18 p.
- Davis, Lawrence S.
1967. Investments in loblolly pine clonal seed orchards: production costs and economic potential. *J. For.* 65: 882-887.
- Davis, Turner S.
1962. Effect of cobalt-60 gamma radiation on pine seed and one-year-old seedlings. *For. Sci.* 8: 411-412.
- Dillon, Elizabeth S., and Bruce J. Zobel.
1957. A simple test for viability of pine pollen. *J. For.* 55: 31-32.
- Dorman, Keith W.
1962. Forest tree improvement for Georgia. *Ga. For. Res. Council. Rep.* 9, 79 p.
1966. Forest tree improvement research in the South and Southeast. *U.S. For. Serv. Res. Pap.* SE-22, 90 p.
——— and John C. Barber.
1956. Time of flowering and seed ripening in southern pines. *USDA For. Serv. Southeast. For. Exp. Stn. Pap.* 72, 15 p.
- Easley, L.T.
1954. Loblolly pine seed production areas. *J. For.* 52: 672-673.
- Echols, R.M., and Francois Mergen.
1956. Germination of slash pine pollen in vitro. *For. Sci.* 2: 321-327.
- Einspahr, Dean W., John R. Peckham and Martin C. Mathes.
1964. Base lines for judging wood quality of loblolly pine. *For. Sci.* 10: 165-173.
——— J.P. van Buijtenen and J.R. Peckham.
1969. Pulp characteristics of ten-year loblolly pine selected for extreme wood specific gravity. *Silvae Genet.* 18: 57-61.
- Franklin, E.C.
1969a. Inbreeding depression in metrical traits of loblolly pine (*Pinus taeda* L.) as a result of self-pollination. *N. C. State Univ. Sch. For. Resour. Tech. Rep.* 40, 19 p.
1969b. Mutant forms found by self-pollination of loblolly pine. *J. Hered.* 60: 315-320.
- Gilmore, A.R.
1957. Physical and chemical characteristics of loblolly pine seedlings associated with drought resistance. *Fourth South. Conf. For. Tree Improv. Proc.* 1957: 34-39.
- Goddard, Ray E., and R.M. Allen.
1955. Controlled pollination techniques. *Third South. Conf. For. Tree Improv. Proc.* 1955: 67-70.
——— and Claud L. Brown.
1959. Growth of drought resistant loblolly pines. *Tex. For. Serv. Res. Note* 23, 7 p.
- Goddard, Ray E., Claud L. Brown and T.E. Campbell.
1959. An evaluation of growth and form in 5-year-old open-pollinated progeny from selected loblolly pine. *Fifth South. Conf. For. Tree Improv. Proc.* 1959: 35-43.
——— and R.K. Strickland.
1964. Crooked stem form in loblolly pine. *Silvae Genet.* 13: 155-157.
- Goggans, J.F., K.D. Lynch and G.I. Garin.
1972. Early results of a loblolly pine seed source study in Alabama. *Auburn Univ. Agric. Exp. Stn. Circ.* 194, 19 p.
- Greene, James T.
1966. Selection for tracheid length in loblolly pine (*Pinus taeda* L.). *Ga. For. Res. Council. Rep.* 18, 30 p.
1969. Variations in height growth and conelet set in two-year-old F₂ seedlings of loblolly pines. *Tenth South. Conf. For. Tree Improv. Proc.* 1969: 92-97.
——— and H.D. Porterfield.
1962. Early cone production in loblolly pine through selection and control pollination. *Ga. Acad. Sci. Bull.* 20: 6.
——— H.D. Porterfield and J.L. Carmon.
1964. Effects of selection and controlled pollinations on the height growth of one-year-old loblolly pines. *Ga. Acad. Sci. Bull.* 22: 41-48.
——— and Mervin Reines.
1958. A preliminary report on field grafting. *J. For.* 56: 127-128.
- Grigsby, Hoy C.
1962. Propagation of loblolly pine by cuttings. *Plant Propagators' Soc. Proc.* 11: 33-35.
1973. A test of 36 geographic sources of loblolly pine seed in southern Arkansas. *USDA For. Serv. Res. Note* SO- (in press).
- Hare, R.C.
1965. Breaking and rooting of fascicle buds in southern pines. *J. For.* 63: 544-546.
——— and G.L. Switzer.

1969. Introgression with shortleaf pine may explain rust resistance in western loblolly pine. USDA For. Serv. Res. Note SO-88, 2 p.
- Hocker, Harold W., Jr.
1955. Climatological summaries for selected stations in and near the southern pine region, 1921-1950. USDA For. Serv. Southeast. For. Exp. Stn. Pap. 56, 11 p.
- Hodgkins, Earl J.
1952. Effect of different heat treatments upon the viability and vigor of pine pollen. J. For. 50: 450-452.
- Hunt, Davie L.
1967. Ninth-year performance of slash and loblolly pine nursery selections in Georgia. Ninth South. Conf. For. Tree Improv. Proc. 1967: 92-94.
- Hyun, Sin Kyu.
1958. Feasibility of large-scale pollination as a means of mass-producing hybrid pine seed. X Int. Congr. Genet. Proc. Vol. II: 130-131.
1970. The growth performance of pitch-loblolly hybrid pine produced by different geographic races of loblolly pine in their early age. FAO/IUFRO Second World Consult. For. Tree Breed. 1969: 803-814. FAO FO-FTB-69 7/7.
Kun Hoe Koo and Kun Yong Ahn.
1965. Some characteristics of backcross hybrids of $\times$ *Pinus rigitaeda*. Inst. For. Genet. Off. Rural Develop., Suwon, Korea, Res. Rep. 4: 11-20.
- Jackson, L.W.R., and W.E. Morse.
1965. Variation in fibril angle of slash and loblolly pine. Ga. For. Res. Council. Res. Pap. 34, 5 p.
- Kais, A.G.
1966. Persistence of albinism in *Cronartium fusiforme*. U.S. Dep. Agric. Plant Dis. Rep. 50: 842.
- Kinloch, Bohun B., Jr., and Roy W. Stonecypher.
1969. Genetic variation in susceptibility to fusiform rust in seedlings from a wild population of loblolly pine. Phytopathology 59: 1246-1255.
- Kormanik, Paul P., Glenn P. Haney and Keith W. Dorman.
1961. Loblolly pine of northern provenance may be best for planting in Virginia. USDA For. Serv. Southeast. For. Exp. Stn. Res. Notes 157, 2 p.
- Kraus, John F.
1967. A study of racial variation in loblolly pine in Georgia—tenth-year results. Ninth South. Conf. For. Tree Improv. Proc. 1967: 78-85.
- Langdon, O. Gordon, Glyndon E. Hatchell and W.P. LeGrande.
1968. Can you top this loblolly pine growth? South. Lumberman 217(2704): 197.
Glyndon E. Hatchell and William P. LeGrande.
1970. Loblolly pine growth topped. South. Lumberman 221(2752): 126-127.
- Lantz, Clark W., and Julian G. Hofmann.
1969. Geographic variation in growth and wood quality of loblolly pine in North Carolina. Tenth South. Conf. For. Tree Improv. Proc. 1969: 175-188.
- Ledig, F. Thomas, and Thomas O. Perry.
1969. Net assimilation rate and growth in loblolly pine seedlings. For. Sci. 15: 431-438.
- Little, Elbert L., Jr., Silas Little and Warren T. Doolittle.
1967. Natural hybrids among pond, loblolly, and pitch pines. USDA For. Serv. Res. Pap. NE-67, 22 p.
and Francis I. Righter.
1965. Botanical descriptions of forty artificial pine hybrids. USDA For. Serv. Tech. Bull. 1345, 47 p.
- Little, S.
1969. Local seed sources recommended for loblolly pine in Maryland and shortleaf pine in New Jersey and Pennsylvania. USDA For. Serv. Res. Pap. NE-134, 16 p.
- McAlpine, Robert G., and L.W.R. Jackson.
1959. Effect of age on rooting of loblolly pine air-layers. J. For. 57: 565-566.
- McLemore, B.F.
1959. Cone maturity affects germination of longleaf pine seed. J. For. 57: 648-650.
- McWilliam, J.R.
1959. Effect of temperature on pollen germination of *Pinus* and its bearing on controlled pollination. For. Sci. 5: 10-17.
- Maple, William R.
1966. Appalachian loblolly grows well in Arkansas Ozarks. USDA For. Serv. Res. Note SO-33, 2 p.
- Marler, R.L.
1963. Economic considerations of the genetic approach. Seventh South. Conf. For. Tree Improv. Proc. 1963: 59-63.
- Mason, R.R.
1967. Dynamics of Ips populations after summer thinning in a loblolly pine (*Pinus taeda*) plantation: with special reference to host tree resistance. (Abstr.) Diss. Abstr. 27B: 2215B.
- Mergen, Francois.
1959. Colchicine-induced polyploidy in pines. J. For. 57: 180-190.
and Lola E. Koerting.
1957. Initiation and development of flower primordia in slash pine. For. Sci. 3: 145-155.
H. Rossoll and K.B. Pomeroy.
1955. How to control pollination of slash and longleaf pine. USDA For. Serv. Southeast. For. Exp. Stn. Pap. 58, 14 p.
and Blanche A. Simpson.
1964. Asexual propagation of *Pinus* by rooting needle fascicles. Silvae Genet. 13: 133-139.
G.R. Stairs and E.B. Snyder.
1965. Natural and controlled loblolly $\times$ shortleaf pine hybrids in Mississippi. For. Sci. 11: 306-314.
- Merrifield, R.G.
1965. Loblolly pine seed sources in north Louisiana. North La. Hill Farm Exp. Stn. For., Hill Farm Facts 6: 4.
- Minckler, Leon S.
1942. One-parent heredity tests with loblolly pine. J. For. 40: 505-506.
- Mohr, Charles.
1897. The timber pines of the southern United States—together with a discussion of the structure of their wood by Filbert Roth. U. S. Dep. Agric. Div. For. Bull. 13, 176 p.
- Namkoong, Gene.
1966. Statistical analysis of introgression. Biometrics 22: 488-502.
- Otterbach, Paul J.
1963. Management of seed orchards. Seventh South. Conf. For. Tree Improv. Proc. 1963: 50-54.
- Pedigo, R.A.
1960. Effects of ionizing radiation on *Pinus taeda*. Ecol. Soc. Am. Bull. 41: 94.
- Perry, Thomas O.
1960. The inheritance of crooked stem form in loblolly pine (*Pinus taeda* L.). J. For. 58: 943-947.
and Chi-Wu Wang.
1957. Collection, shipping, and storage of slash and loblolly pine cuttings. J. For. 55: 122-123.
- Reines, Mervin.
1963. The influence of age of clonal parent on rooting of needle bundles. Ga. For. Res. Council. Res. Pap. 16, 3 p.
and James T. Greene, Jr.
1956-57. Forest genetics at the George Foster Peabody School of Forestry. Ga. For. Res. Council. Rep. 5, 24 p.
- Saucier, J.R., and M.A. Taras.
1969. Regional variation in specific gravity of seven pines in the southern United States. U.S.D.A. For. Serv. Res. Pap. SE-45, 16 p.
- Saylor, L.C.
1961. A karyotypic analysis of selected species of *Pinus*. Silvae Genet. 10: 77-84.
1967. Variability of chromosome structure and behavior in southern pine hybrids. Ninth South. Conf. For. Tree Improv. Proc. 1967: 95-100.
- Schmitt, Dan.
1968. Performance of southern pine hybrids in south Mississippi. USDA For. Serv. Res. Pap. SO-36, 15 p.
- Shelbourne, C.J.A.
1967. Studies on the inheritance and relationship of bole straight-

- ness and compression wood in southern pines. Ph.D. Thesis, N. C. State Univ. 274 p.
- Shelbourne, C.J.A., and G. Namkoong.
1966. Photogrammetric technique for measuring bole straightness. Eighth South. Conf. For. Tree Improv. Proc. 1965: 131-136.
- B.J. Zobel and R.W. Stonecypher.
1969. The inheritance of compression wood and its genetic and phenotypic correlations with six other traits in five-year-old loblolly pine. *Silvae Genet.* 18: 43-47.
- Smouse, Peter.
1970. Population studies in the genus *Pinus*. Ph.D. Thesis, N. C. State Univ. 126 p.
- Snow, A.G., Jr., K.W. Dorman and C.S. Schopmeyer.
1943. Development stages of female strobili in slash pine. *J. For.* 41: 922-923.
- Snyder, E. Bayne.
1961. Extracting, processing, and storing southern pine pollen. USDA For. Serv. South. For. Exp. Stn. Occas. Pap. 191, 14 p.
- H.C. Grigsby and J.U. Hidalgo.
1961. X-radiation of southern pine seed at various moisture contents. *Silvae Genet.* 10: 125-131.
- and A.E. Squillace.
1966. Cone and seed yields from controlled breeding of southern pines. USDA For. Serv. Res. Pap. SO-22, 7 p.
- Southeastern Forest Experiment Station.
1962. Report for 1961. USDA For. Serv., 81 p.
- Stanley, R.G., J. Peterson and N.T. Mirov.
1960. Viability of pine pollen stored 15 years. USDA For. Serv. Pac. Southwest For. & Range Exp. Stn. Res. Note 173, 5 p.
- Stonecypher, R.W.
1966. The loblolly pine heritability study. Int. Pap. Co., Southlands Exp. For. Tech. Bull. 5, 128 p.
- Franklin C. Cech and Bruce J. Zobel.
1964. Inheritance of specific gravity in two- and three-year-old seedlings of loblolly pine. *Tappi* 47: 405-407.
- Thames, John L.
1962. Loblolly best, but seed source important in erosion-control plantings in north Mississippi. USDA For. Serv. Tree Plant. Notes 55: 21-22.
1963. Needle variation in loblolly pine from four geographic seed sources. *Ecology* 44: 168-169.
- Thor, Eyvind.
1967. A ten-year-old loblolly pine seed source test in Tennessee. *J. For.* 65: 326-327.
- and Shelby J. Brown.
1962. Variation among six loblolly pine provenances tested in Tennessee. *J. For.* 60: 476-480.
- Thorbjornsen, Eyvind.
1960. A cone production study in loblolly pine on the Coastal Plain of North Carolina. *J. For.* 58: 543-547.
- Trousdell, K.B., Keith W. Dorman and A.E. Squillace.
1963. Inheritance of branch length in young loblolly pine progeny. U.S. For. Serv. Res. Note SE-1, 2 p.
- USDA Forest Products Laboratory.
1965. Southern wood density survey—1965 status report. USDA For. Serv. Res. Pap. FPL-26, 38 p.
- USDA Forest Service.
1948. Woody-plant seed manual. USDA For. Serv. Misc. Publ. 654, 416 p.
- van Buijtenen, J.P.
1963. Inheritance of wood properties and their relation to growth rate in *Pinus taeda*. FAO World Consult. For. Genet. Tree Breed. Proc. 1963. FAO Forgen 63/ -7/2.
1964. Anatomical factors influencing wood specific gravity of slash pines and the implications for the development of a high-quality pulpwood. *Tappi* 47: 401-404.
1966. Testing loblolly pines (*Pinus taeda*) for drought resistance. Tex. For. Serv. Tech. Rep. 13, 15 p.
1969. Seventeenth progress report of the cooperative forest tree improvement program. Tex. For. Serv. Circ. 200, 14 p.
- VanHaverbeke, David F., and John C. Barber.
1964. Seed crop estimation in a loblolly pine seed production area. Ga. For. Res. Council. Res. Pap. 21, 5 p.
- Wahlenberg, W.G.
1960. Loblolly pine. 603 p. Duke Univ. Sch. For. ——— and C.E. Ostrom.
1956. Geographic variation in climate in the loblolly pine region. USDA For. Serv. Southeast. For. Exp. Stn. Res. Notes 94, 2 p.
- Wakeley, Philip C.
1954. Planting the southern pines. USDA For. Serv. Agric. Monogr. 18, 233 p.
1961. Results of the southwide pine seed source study through 1960-61. Sixth South. Conf. For. Tree Improv. Proc. 1961: 10-24.
- and T.E. Bercaw.
1965. Loblolly pine provenance test at age 35. *J. For.* 63: 168-174.
- Wasser, Ronald G.
1967. A shortleaf and loblolly pine flowering phenology study. Va. Div. For. Occas. Rep. 28, 2 p.
- Webb, C.D.
1961. Field grafting loblolly pine. N. C. State Coll. Sch. For. Tech. Rep. 10, 33 p.
- Wells, Delmus Wayne, and M. Reines.
1965. Vegetative propagation of needle bundles of pines. Ga. For. Res. Council. Res. Pap. 26, 8 p.
- Wells, Osborn O.
1966. Variation in rust resistance among pine seed sources and species in a Mississippi planting. *For. Sci.* 12: 461-463.
1969. Results of the southwide pine seed source study through 1968-69. Tenth South. Conf. For. Tree Improv. Proc. 1969: 117-129.
- and G.L. Switzer.
1971. Variation in rust resistance in Mississippi loblolly pine. Eleventh South. Conf. For. Tree Improv. Proc. 1971: 25-30.
- and Philip C. Wakeley.
1966. Geographic variation in survival, growth, and fusiform-rust infection of planted loblolly pine. *Soc. Am. For., For. Sci. Monogr.* 11, 40 p.
- Whitesell, Craig D., Bruce J. Zobel and James Roberds.
1966. Specific gravity and tracheid length of loblolly pine in Maryland and Delaware. N. C. State Univ. Sch. For. Tech. Rep. 29, 11 p.
- Woerheide, John D.
1959. Loblolly seed from Maryland best of six sources tested in southern Illinois. USDA For. Serv. Cent. States For. Exp. Stn. Note 129, 2 p.
- Woessner, Ronald A.
1965. Growth, form, and disease resistance in four-year-old control- and five-year-old open-pollinated progeny of loblolly pine selected for use in seed orchards. N. C. State Univ. Sch. For. Tech. Rep. 28, 67 p.
- Youngman, A.L.
1967. An ecotypic differentiation approach to the study of isolated population of *Pinus taeda* in south central Texas. (Abstr.) *Diss. Abstr.* 27B(9): 3006.
- Zarger, Thomas G.
1961. Ten year results on a cooperative loblolly pine seed source test. Sixth South. Conf. For. Tree Improv. Proc. 1961: 45-52.
- Zarger, Thomas G.
1965. Performance of loblolly, shortleaf, and eastern white pine superseedlings. *Silvae Genet.* 14: 182-186.
- Zobel, Bruce J.
1952. Abnormal cone formation in pines. *Tex. J. Sci.* 4: 517-520.
1953. Are there natural loblolly-shortleaf pine hybrids? *J. For.* 51: 494-495.
1961. Inheritance of wood properties in conifers. *Silvae Genet.* 10: 65-70.
1964. Breeding for wood properties in forest trees. *Unasylva* 18 (2/3): 89-103.
- Roger Blair and Marvin Zoerb.
1971. Using research data—disease resistance. *J. For.* 69: 486-489.
- and Ray E. Goddard.

1955. Preliminary results on tests of drought hardy strains of loblolly pine (*Pinus taeda* L.). Tex. For. Serv. Res. Note 14, 23 p.
- Zobel, Bruce J., Ray E. Goddard and Franklin C. Cech.
1957. Outstanding nursery seedlings—a progress report. Tex. For. Serv. Res. Note 18, 14 p.
- _____. Robert Kellison and Martha Matthias.
1969. Genetic improvement in forest trees—growth rate and wood characteristics in young loblolly pine. Tenth South. Conf. For. Tree Improv. Proc. 1969: 59-75.
- _____. and R.L. McElwee.
1958. Variation of cellulose in loblolly pine. Tappi 41: 167-170.
- _____. and R.L. McElwee.
1964. Seed orchards for the production of genetically improved seed. *Silvae Genet.* 13: 4-11.
- _____. Martha Matthias, James H. Roberds and R.C. Kellison.
1967. Moisture content of southern pine trees. Fourth For. Biol. Conf. Proc. 1967: 11-35.
- _____. and R.R. Rhodes.
1955. Relationship of wood specific gravity in loblolly pine to growth and environmental factors. Tex. For. Serv. Tech. Rep. 11, 32 p.
- _____. R.W. Stonecypher and Cicely Browne.
1967. Inheritance of spiral grain in young loblolly pine. Ninth South. Conf. For. Tree Improv. Proc. 1967: 129.
- _____. R.W. Stonecypher, C. Browne and R.C. Kellison.
1966. Variation and inheritance of cellulose in the southern pines. Tappi 49: 383-387.
- _____. Eyvind Thorbjornsen and Faye Henson.
1960. Geographic, site and individual tree variation in wood properties of loblolly pine. *Silvae Genet.* 9: 149-158.
- Zoerb, M.H., Jr.
1969. Clonal variation in time of cone ripening in loblolly pine. Union Camp Corp., Woodlands Res. Dep., Woodlands Res. Note 22, 3 p.

Dorman, Keith W., and Zobel, Bruce J.

1973. Genetics of loblolly pine. USDA For. Serv. Res. Pap. WO-19, 21 p.

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